

Foraging Ecology of Lesser Long-nosed Bats

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Final Report

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Executive Summary

We initiated this study to develop a better understanding of the relationship between endangered lesser long-nosed bats, *Leptonycteris curasoae*, and their food resources. Many thousand lesser long-nosed bats migrate from Mexico to southern Arizona each summer. Their diet consists of nectar, pollen, and fruit from a variety of plants. During their residency in southeastern Arizona, however, the bats consume primarily nectar and pollen from a single species of plant, *Agave palmeri*.

We radiotracked 60 female lesser long-nosed bats during two summers to assess their use of the landscape and the density of primary food resources (*Agave palmeri*) at two spatial scales: within their home ranges (defined as 95% kernel areas) and within their core use-areas (defined as 50% kernel areas). Bats commuted an average of 18.9 km (SE = 1.2) from day roosts to core use-areas, where they spent the majority of each night within areas that often overlapped those of other bats. Density ($\bar{x} \pm \text{SE}$ plants/ha) of flowering *A. palmeri* within bat home ranges (3.5 ± 0.4) exceeded that which was available on the landscape (1.9 ± 0.4), suggesting that bats selected areas with high resource abundance. Density of dead standing *A. palmeri* within home ranges (3.9 ± 1.2) also exceeded that which was available on the landscape (1.2 ± 0.2), suggesting that bats selected areas that had high resource abundance previously, and also that bats may exhibit site fidelity to *A. palmeri* patches.

Annual differences in abundance of food resources were associated with variation in bat activities. Density ($\bar{x} \pm \text{SE}$) of flowering *A. palmeri* within adult home ranges was much higher in 1998 (3.5 ± 0.4) than in 1999 (0.8 ± 0.2). This difference was associated with adults leaving day roosts much later in 1998 (129 ± 15 min after sunset) than in 1999 (57 ± 12). However, size of adult home ranges (1998: 3040 ± 879 ha; 1999: 2267 ± 426 ha) and core use-areas (1998: 21 ± 5 ha; 1999: 16 ± 2 ha) was similar between years. Furthermore, we found no relationship between density of food resources and home-range size ($r^2 = 0.01$, $P = 0.77$). Because individual flowering agaves provide a large quantity of resources, use by bats may not reflect small patterns of changes in resource abundance at the landscape scale.

We examined smaller-scale patterns of foraging behavior of bats by determining associations between structural and spatial characteristics of *A. palmeri* and rates of bat visitation to individual plants. We assessed the association between 8 plant characteristics and bat visitation rates, which varied considerably among plants and at the same plant throughout a night. In general, bat visitation rates to plants were associated with variation in resource abundance at several spatial and temporal scales. Specifically, visitation rates of bats to plants were associated with variation in time of night, distance and direction from roost, and number and relative vertical position of flowering umbels. Each of these factors is related directly to either the amount of nectar available to pollinators or to the location of plants relative to the bats' roost.

We investigated energetic requirements of lesser long-nosed bats by measuring their time-activity budgets. High annual variability in nectar availability greatly influenced the ability of bats to meet their energetic needs. Bats spent 66% less time roosting and 120% more time foraging during the year when resource abundance was low than they did during the year food was more abundant. Presumably bats needed to spend more time foraging when fewer flowering plants were present. We estimated energy requirements for bats and determined the amount of energy available from *A. palmeri* inflorescences. One bat required 14.59 kcal/day in 1998 and 21.91 kcal/day in 1999, and the average amount of energy available from the bats' primary food source is 3277 kcal/plant over the course of a flowering season.

Given the amount of time bats spend in southeastern Arizona and the length of the *A. palmeri* flowering season, we estimate that one *A. palmeri* produces enough nectar to support approximately 1.5 bats throughout the time they inhabit the region.

Lesser long-nosed bats are highly dependent on *A. palmeri* during their residence in Southern Arizona. Because this resource is distributed patchily and the number of flowering plants varies greatly from year to year, recovery of this endangered bats is inextricably linked to conservation of this food source. We found evidence that bats select areas with both high resource abundance and evidence of high resource abundance in previous years, suggesting site fidelity to *A. palmeri* stands. The seasonal dietary specialization of lesser long-nosed bats implies that a reduction in or further fragmentation of *A. palmeri* populations could have serious effects on bat behavior, forcing them to commute farther, roost in substandard roosts, or compete with one another for food at remaining plants. These changes could eventually have adverse effects on the Arizona population of lesser long-nosed bats, especially in years of lower flower production, when energy expended by bats is appreciably higher. Finally, because bats use resources spread across large geographic areas, landowners must work cooperatively to meet the mandates of bat recovery and conservation. Maintaining sufficient numbers of *Agaves* as a food source for bats and other nectivores is likely more important and challenging than thought previously.

Introduction

The quantity and quality of plants as a resource for animals varies over both space and time (Hunter et al. 1992). Variability in the distribution and abundance of plants influences the distribution and abundance of those animals that rely on these plants. Animals capable of flight can locate highly dispersed plant patches and select those that are most rewarding. Flight entails a high energetic cost, however, so flying pollinators need to consume large quantities of food, and consequently must either visit many plant patches, patches with many plants, or locate highly rewarding plants within each patch.

Distribution and migration of lesser long-nosed bats, *Leptonycteris curasoae*, coincide with distribution and phenology of flowering agaves, suggesting a mutualistic relationship (Howell and Roth 1981, Fleming et al. 1993). During late summer in southeastern Arizona, agave nectar and pollen account for >90% of foods for these bats (Beatty 1955, Hayward and Cockrum 1971, Howell 1972, Hevly 1979). Timing of flowering may influence foraging patterns of bats, which may influence the probability of cross-pollination among plants, which in turn may influence their distribution in the long-term (Heithaus et al. 1975, Schaffer and Schaffer 1979).

Lesser long-nosed bats were listed as endangered in the United States in 1988 (Shull 1988) and in Mexico in 1991 (USFWS 1995). Two interdependent habitat components recognized as critical to recovery of this species are suitable day roosts and concentrations of forage plants (USFWS 1995). Consequently, interrelationships between these two resources must be understood to assess how best to manage lands to foster recovery of these endangered bats.

Study Area

Our study took place in Cochise County, Arizona (31°30'N, 110°20'W), in an area defined by the Patagonia Mountains to the west, the Mustang Mountains to the north, the Huachuca Mountains to the east, and the Mexican border to the south. Elevation varied from a minimum of 1400 m in grasslands to maximums of 1972, 2201, and 2885 m in the Mustang, Patagonia, and Huachuca Mountains, respectively.

Precipitation is bimodal with significant rainfall in summer (July-October) and winter (December-March). From late June to early September, the area receives frequent, brief localized thunderstorms in the afternoon or evening. Annual precipitation at Fort Huachuca averaged 391 mm between 1900 and 1982, with an average of 88 mm in August and 44 mm in September (Sellers et al. 1985). Daily maximum and minimum temperatures averaged 30.7 and 17.4 °C in August and 29.2 and 15.4 °C in September (Sellers et al. 1985).

Vegetation between 1500 and 1700 m is semidesert grassland, characterized by perennial grass-
scrub, and at higher elevations is Madrean evergreen woodland, characterized by oaks, junipers, and pinyon (Brown 1982). *A. palmeri* is found in scattered patches between 930 and 1850 m elevation, primarily in xeric sites with rocky soils (Gentry 1982).

Part I: Resource Abundance and Habitat Use

We investigated movements of lesser long-nosed bats to determine how spatial variability in resource abundance affects foraging behavior and habitat use of bats. Our specific objectives were to determine locations and sizes of home ranges and core use-areas of individual bats, estimate density and distribution of nectar-producing *A. palmeri* within home ranges and across the landscape, and determine if activity and spatial-use patterns of bats reflect patterns of food abundance.

METHODS

Bat Movements

We investigated nocturnal travel patterns of lesser long-nosed bats with radio telemetry during August and September, 1998 and 1999. We captured bats while nightroosting (Table 1), and determined sex, age, body mass, and reproductive status before attaching radio transmitters to 30 females each year. Two transmitter models of different mass were used (model BD-2A, 0.69-0.85g; model BD-2, 0.93 g; Holohil Systems, Ltd.), with life expectancies ranging from 3 to 6 weeks. Transmitter mass averaged 3.2% and 2.9% of body mass in 1998 and 1999 respectively. We trimmed fur from the bats' upper backs and affixed transmitters with Skinbond Medical Adhesive, Hollister Medical Adhesive, or NuHope Medical Adhesive.

We captured and tracked bats during two consecutive sessions each year. During each session, we monitored movements of bats from a network of tracking stations throughout the study area. Field personnel equipped with a compass, receiver, and 3- or 5-element Yagi antenna scanned all frequencies continuously from sunset to sunrise. When observers detected a bat they notified others via two-way radio and recorded bearings on that bat simultaneously for 3 consecutive minutes.

Transmitter locations were deduced from bearings taken concurrently from 2 or more tracking stations using Lenth's (1981) maximum likelihood estimator (LOCATE II, Nams 1996). Error ellipses were computed for all fixes calculated from >2 simultaneous bearings. Because error ellipses cannot be computed for fixes estimated from 2 bearings, we discarded all locations based on 2-bearing fixes that were >10 km from observers or fixes that were >2 km from previous and subsequent locations.

We determined accuracy of observer bearings by placing reference transmitters in several locations unknown to field personnel and compared estimates to true locations. Standard deviations of diversions of bearings were pooled to derive a mean standard deviation ($\bar{x} = 5^\circ$) which was used to calculate error ellipses.

We determined bat use of the landscape at two scales. For an overview bat use-patterns, we calculated home ranges, which we defined as the smallest area in which 95% of all locations for each individual throughout the study period with error polygons <1600 ha. For a more accurate assessment of areas bats used frequently, we calculated core use-areas, which we defined as the smallest area that accounted for 50% of locations collected for each individual throughout the study period, using only locations based on >2 simultaneous bearings with error polygons <200 ha. We calculated sizes of home ranges and core use-areas using minimum convex polygon (MCP) (Mohr 1947) and fixed-kernel (Worton 1989) methods (RANGES V, Kenward and Hodder 1996). We report MCP to facilitate comparisons with other studies (Harris et al. 1990). We also used MCP to estimate the extent of overlap between

Table 1. Dates and locations of lesser long-nosed bat captures, southeastern Arizona.

Date	Location	No. bats captured
15 Aug 1998	Wren Bridge, Fort Huachuca	2
16 Aug 1998	Wren Bridge, Fort Huachuca	0
17 Aug 1998	Manilla Mine, Fort Huachuca	27
29 Aug 1998	Anderson Mine, west of Fort Huachuca	38
12 Aug 1999	Anderson Mine, west of Fort Huachuca	11
13 Aug 1999	Anderson Mine, west of Fort Huachuca	22
26 Aug 1999	Anderson Mine, west of Fort Huachuca	13
27 Aug 1999	Anderson Mine, west of Fort Huachuca	10

individual bat home ranges and core use-areas. The cross-validated fixed-kernel method also was used because it has been shown to provide area estimates with little bias and low error (Worton 1995, Seaman and Powell 1996).

We computed nightly commute distances for each bat whose day roost location was known. This distance was defined as the span between the day roost and the geometric center of the core use-area (Hayne 1949).

Bat Activity Patterns

We determined the time bats emerged from and returned to day roosts on 11 nights. We also determined the percentage of the night each bat spent away from the roost, which we defined as the ratio of the number of minutes between emergence and return to the number of minutes between sunset and sunrise, multiplied by 100.

Agave Density

We estimated densities of *A. palmeri* to assess food resources available to bats using variable-width line-transect methods (Buckland et al. 1993) to estimate *A. palmeri* densities within home ranges each year and across the landscape in 1998. We walked 77.6 km of transects located within and adjacent to bat home ranges in 1998 and 39.5 km of transects located within bat home ranges in 1999. We measured distances from the transect to flowering *A. palmeri* and to dead standing *A. palmeri* inflorescences. We determined densities of dead standing *A. palmeri* inflorescences, which remain standing for one to several years after flowering, to estimate previous food abundance in areas used by bats. We calculated densities of both live and dead standing *A. palmeri* inflorescences combined, as density of all standing stalks might provide a visual cue of resource abundance to bats.

Statistical Analyses

We compared commute distances, percentage of the night spent away from day roosts, emergence times, return times, sizes of home-ranges and core use-areas, and densities of flowering and dead standing *A. palmeri* inflorescence within home ranges between bats caught in different years and between juvenile and adult bats using *t*-tests. Data were square-root, reciprocal, or natural log transformed when necessary, however means and standard errors are reported on the scale of original measurement. If we failed to detect a difference between groups, we calculated a posteriori power (and associated 90% confidence intervals) to detect a 20% difference between groups for $\alpha = 0.10$ (Steidl et al. 1997). We used simple linear regression to determine if the distribution of lesser long-nosed bat home-range sizes was related to the densities of live, dead standing, or live and dead standing *A. palmeri*.

RESULTS

In 1998, we tracked 28 adult and 2 juvenile females from 1 to 15 nights each ($\bar{x} = 4.3$, $SE = 0.7$). Nineteen individuals were tracked for ≥ 3 nights, and 9 bats were never detected after the night transmitters were attached. In 1999, we tracked 25 adult and 5 juvenile females from 1 to 17 nights each ($\bar{x} = 7.6$, $SE = 0.5$). Twenty-six bats were tracked for ≥ 3 nights, and all bats detected after the night transmitters were attached. We collected 50,792 bearings during approximately 2,650 person-hours of tracking over 49 nights.

Bat Commuting Behavior

Although all bats within each session were captured at the same night roost, individuals used at least five different day roosts. The three day roosts used by the majority of bats ($n = 37$) were located 27.8, 41.0, and 42.9 km from one another (Fig. 1). In 1998, each individual returned to the same day roost for the duration of our study, and in 1999 27% of bats ($n = 8$ of 30) changed day roost sites.

Upon exiting day roosts in the evening, bats flew directly to their core use-areas where they spent the majority of the night before commuting back to day roosts in the morning. The straight-line commute distance from day roosts to core use-areas for bats in 1998 averaged 17.2 km ($SE = 5.1$, $n = 4$); for bats using only one core use-area in 1999, commute distance averaged 20.6 km ($SE = 1.4$, $n = 11$). Commute distances for bats that switched core use-areas in 1999 averaged 19.2 km ($SE = 0.02$, $n = 3$) before the switch and 13.8 km ($SE = 4.4$, $n = 3$) after the switch. Mean commute distance did not differ between

Table 2. Commute distances (km) of lesser long-nosed bats from day roosts to core-use areas, southeastern Arizona, 1998 and 1999.

Year	Age	<i>n</i>		SE	Range
1998	Adult	4	17.2	5.1	2.8 - 27.2
1999	Adult	14	19.6	1.5	7.5 - 28.2
1999	Juvenile	5	18.5	3.9	11.8 - 22.2
Overall	Adult and Juvenile	23	18.9	1.2	2.8 - 28.2

Table 3. Amount of time and percentage of each night lesser long-nosed bats spent away from day roosts, southeastern Arizona, 1998 and 1999.

Year	Age	<i>n</i>	No. hours			% of each night		
			\bar{x}	SE	Range	0	SE	Range
1998	Adult	8	7.1	0.3	5.5 - 8.3	63	2.9	48 - 73
1998	Juvenile	1	8.1	-	-	74	-	-
1999	Adult	8	7.2	0.2	6.4 - 7.7	67	1.3	60 - 71
1999	Juvenile	2	8.8	0.3	8.6 - 9.1	82	1.8	80 - 83
Overall	Adult and Juvenile	19	7.4	0.2	5.5 - 9.1	67	1.8	48 - 83

adults caught different years (two-sample *t*-test, $t_{16} = -0.62$, $P = 0.54$) or between juveniles and adults caught in 1999 (two-sample *t*-test, $t_{17} = 0.39$, $P = 0.70$). Commute distance for all individuals averaged 18.9 km (SE = 1.2, $n = 23$) (Table 2).

Bat Activity Patterns

The amount of time bats spent out of day roosts ranged from a minimum of 5 hrs 27 min to a maximum of 9 hrs 3 min per night, which represents 48 to 83% of the time between sunset and sunrise (Table 3). Mean percentage of the night spent away from day roosts and mean time of return to day roosts did not differ appreciably between adult bats in different years ($P \geq 0.28$) (Tables 3, 4). However, emergence times from day roosts differed considerably between years (two-sample *t*-test, $t_{20} = 3.79$, two-sided $P = 0.001$). Adults emerged from day roosts an average of 73 min (SE = 19) later in 1998 than in 1999 (Table 4).

Bat Home Ranges and Core Use-Areas

Home-range sizes (95% kernel) ranged vastly, from 174 to 5258 ha (Table 5). Adult home-range sizes were similar between years (two-sample *t*-test, $t_{19} = 0.79$, two-sided $P = 0.44$; power = 0.16, 90% C.I. = 0.13–0.19), averaging 773 ha (SE = 977) larger in 1998 than in 1999. Home range of juvenile bats averaged 1125 ha (SE = 898) less than adults, but because of high variability, did not differ significantly (two-sample *t*-test, $t_{19} = 1.25$, $P = 0.23$; power = 0.14, 90% C.I. = 0.12–0.17). Night roosts were located within or near bat home ranges.

Core use-area sizes (50% kernel) ranged from 3 to 42 ha (Table 6). Adult core use-area sizes were similar between years (two-sample *t*-test, $t_{19} = 1.06$, two-sided $P = 0.30$; power = 0.19, 90% C.I. = 0.15–0.24), averaging 6 ha (SE = 5) larger in 1998 than in 1999. Core use-areas of juvenile bats

averaged 9 ha (SE = 5) larger than those of adults (two-sample *t*-test, $t_{19} = -1.87$, $P = 0.08$; power = 0.16, 90% C.I. = 0.13–0.20) (Table 6).

Table 4. Timing of emergence from (no. min after sunset) and return to (no. min before sunrise) day roosts by lesser long-nosed bats, southeastern Arizona, 1998 and 1999.

Year	Age	Emergence times				Return times			
		<i>n</i>	\bar{x}	SE	Range	<i>n</i>	\bar{x}	SE	Range
1998	Adult	9	129	21	45 - 205	10	140	14	53 - 214
1998	Juvenile	1	72	-	-	1	100	-	-
1999	Adult	13	56	7	25 - 105	8	144	8	108 - 169
1999	Juvenile	5	45	6	33 - 67	2	60	19	41 - 78
Overall	Adult and Juvenile	28	78	10	25 - 205	21	132	9	41 - 214

Although bats spent days at roosts located up to 42.9 km from one another (Fig. 1), they foraged in home ranges and core use-areas that overlapped (Fig. 2). The maximum extent of overlap between home ranges was 100% and between core use-areas 44%. When considered in pairs, 70% of home-range pairs (62 of 89) overlapped; of those that did, average overlap was 41% (SE = 3). In contrast, only 6% of core use-area pairs (5 of 89) overlapped; of those that did, average overlap was 19% (SE = 6).

Agave Density

Density of flowering *A. palmeri* across the landscape was much greater in 1998 than in 1999, which was reflected in density of plants within home ranges of adult bats (Table 7). Accordingly, density of flowering plants within adult home ranges in 1998 exceeded that in 1999 (two-sample *t*-test, $t_{19} = 5.79$, two-sided $P < 0.0001$) by an average of 2.7 (SE = 0.5) plants/ha. In 1998, density ($\bar{x} \pm$ SE plants/ha) of flowering *A. palmeri* in home ranges of adults (3.5 ± 0.4) was much greater than that available on the landscape (1.9 ± 0.4).

Density of dead standing inflorescences within bat home ranges in 1998 was similar to that in 1999 (two-sample *t*-test, $t_{19} = 0.48$, two-sided $P = 0.63$) (Table 7). In 1998, density of dead standing *A. palmeri* inflorescences in adult home ranges (3.9 ± 1.2) was much greater than that available on the landscape (1.2 ± 0.2).

Density of both live and dead standing *A. palmeri* inflorescences combined was greater in home ranges of adults in 1998 than in 1999 (two-sample *t*-test, $t_{19} = 1.85$, $P = 0.08$), with density an average of 2.2 (SE = 1.2) plants/ha greater in 1998 than in 1999 (Table 7). Lastly, in 1999, densities of flowering *A. palmeri*, dead standing *A. palmeri*, and both combined were similar within home ranges of adults and juveniles ($P \geq 0.66$, Table 7).

Home-Range Size and Resource Abundance

Home-range size did not vary with changes in density of flowering *A. palmeri* ($F_{1,15} = 0.09$, $P = 0.77$)

or with density of both live and dead standing *A. palmeri* inflorescences combined ($F_{1,15} = 2.62$, $P = 0.13$) among adults in 1999. However, home-range size decreased with increasing density of dead standing *A. palmeri* inflorescences ($F_{1,15} = 4.69$, $P = 0.05$) for adult bats in 1999 (Fig. 3).

DISCUSSION

Pollination is a mutualistic plant-animal interaction. In the process of obtaining carbohydrates from nectar, animals facilitate outbreeding among plants by transporting pollen. Bats consume large amounts of nectar and are therefore energetically expensive to plants relative to smaller pollinators. For plants, however, the cost of producing enough nectar to attract bats is likely offset by the genetic advantage they obtain from the long-distance pollen dispersal which bats provide. Pollinators capable of long-distance dispersal are especially important to the promotion of outbreeding among patchily distributed plants, such as *A. palmeri*. Two factors ensure high visitation rates of bats to *A. palmeri* flowers. First, large amounts of food need to be provided by plants to meet the energy demands of lesser long-nosed bats, which typically consume 150% of their body mass in nectar per night in captivity (Winter and von Helversen 1998). Second, the small size of *A. palmeri* flowers allows only a small amount of nectar to be produced per flower, forcing bats to visit many flowers. Because lesser long-nosed bats visit *A. palmeri* flowers exclusively during late summer in southeastern Arizona, the prospect of pollen reaching conspecific plants is favorable.

Predictability of nectar availability varies in space and time. *A. palmeri* flowers produce nectar for 5 consecutive nights before wilting, each plant may produce 1600-2240 flowers over the course of the flowering season (Slauson 1999), and time between the first flower blooming to the last flower wilting on asynchronous among plants within a population. Therefore, nectar availability changes over the course a single inflorescence is approximately 40 days (Howell and Roth 1981). Furthermore, flowering is of several weeks, but not over the course of several days. This likely explains why we observed bats returning to the same core use-areas on consecutive nights. Similar patterns have been reported for lesser long-nosed bats in Sonora, Mexico (Horner et al. 1998), for other nectarivorous bats such as *Glossophaga soricina* (Lemke 1984), frugivorous bats such as *Carollia perspicillata* (Heithaus and Fleming 1978), and insectivorous bats such as *Plecotus townsendii* (Dobkin et al. 1995), *Eptesicus nilssoni* (De Jong 1994), and *Macroderma gigas* (Tidemann et al. 1985). Because areas rich in food resources one night are likely to be rich in food the following night, returning to the same area eliminates the energy expenditure required to search for new flowering plants.

Because mobile animals are able to encounter and sample food from a large area, occasional responses to changes in food resources are likely. We observed seven bats abruptly change from one core use-area to another. Once a new area was visited, we never observed bats returning to the original area. These changes in core use-areas tended to coincide with the cessation of nectar production from *A. palmeri* in the original area (pers. obs.).

Bats flew an average straight-line commute distance of 18.9 km, which is relatively long in comparison to most bat species, but less than has been reported for lesser long-nosed bats elsewhere. For example, lesser long-nosed bats commuted an average of 27.2 km one way near Bahio Kino, Sonora, Mexico, when they fed on columnar cacti (Sahley et al. 1993). Scarcity of appropriate day roosts likely explains the bats' long commute distances. Lesser long-nosed bats require warm roosting areas deep

Table 5. Home-range sizes of lesser long-nosed bats, southeastern Arizona, 1998 and 1999.

Year	Age	n	No. locations			No. nights tracked			95% MCP (ha)			95% Kernel (ha)		
			mean	SE	Range	mean	SE	Range	mean	SE	Range	mean	SE	Range
1998	Adult	4	256	86	59-462	8	1.5	4-11	4993	1606	1000-8206	3040	949	548-4997
1999	Adult	17	200	38	25-611	5	0.5	2-9	1965	475	161-6217	2267	420	174-5258
1999	Juvenile	4	229	45	123-311	4	0.9	2-6	1046	309	328-1717	1142	369	448-2141
Overall	Adult and Juvenile	25	213	29	25-611	5	0.5	2-11	2222	448	161-8206	2211	336	174-5258

Table 6. Core use-area sizes of lesser long-nosed bats, southeastern Arizona, 1998 and 1999.

Year	Age	n	No. locations			No. nights tracked			50% MCP (ha)			50% Kernel (ha)		
			mean	SE	Range	mean	SE	Range	mean	SE	Range	mean	SE	Range
1998	Adult	4	28	13	8-64	4	1.3	1-7	15	11	2-49	21	7	11-42
1999	Adult	17	107	22	14-365	4	0.4	1-8	9	3	1-53	16	2	3-33
1999	Juvenile	4	133	34	63-193	4	0.6	2-5	13	3	6-21	25	5	12-35
Overall	Adult and Juvenile	25	98	17	8-365	4	0.3	1-8	11	3	1-53	18	2	3-42

Figure 1, Map of study area in southeastern Arizona, showing locations of home ranges, the three major day roost sites, and the capture location of lesser long-nosed bats, 1998 and 1999.

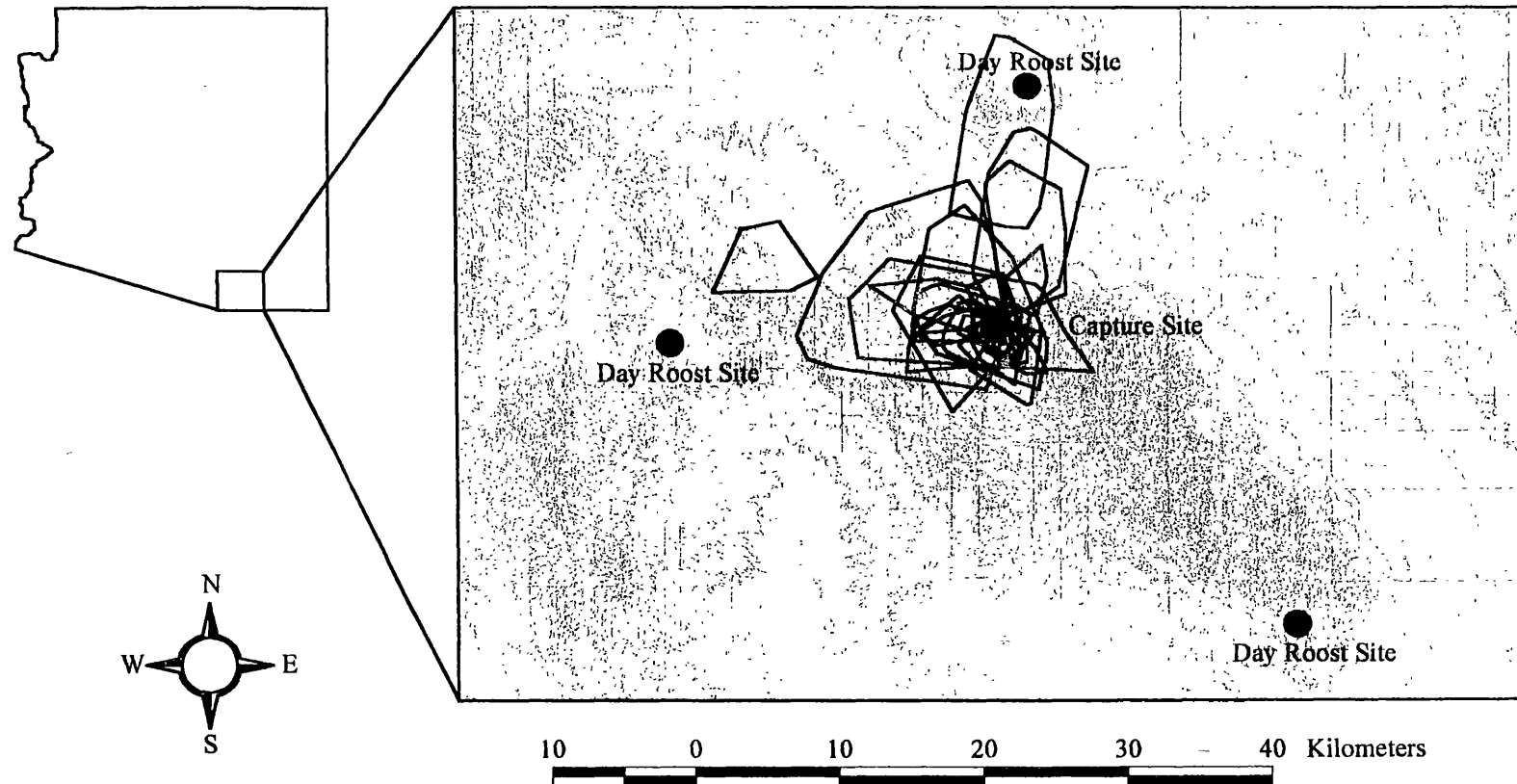
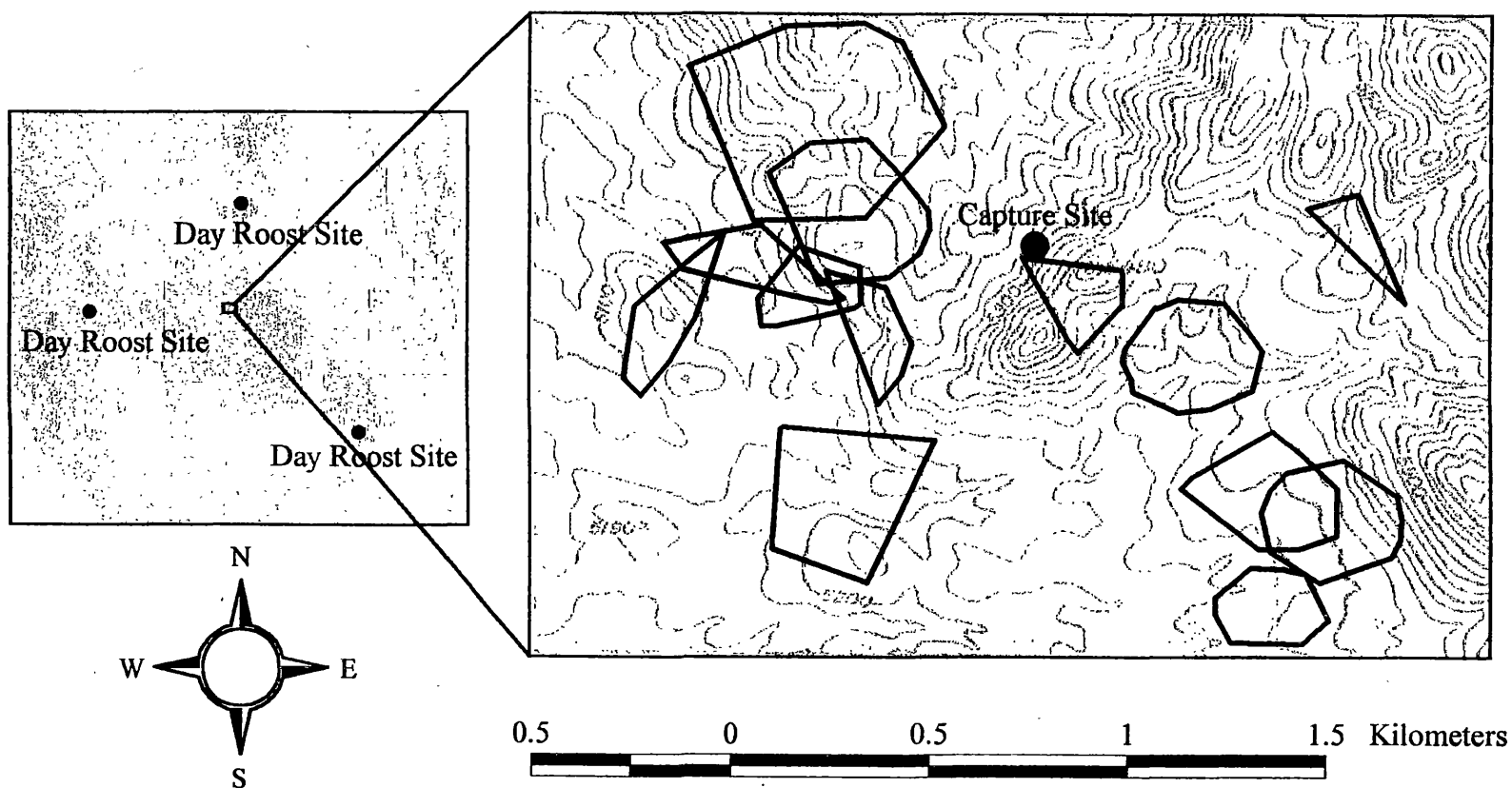


Figure 2, Map showing overlap of several core use-areas of lesser long-nosed bats, southeastern Arizona, 1998 and 1999.



inside caves and mines. The warmth provided by cave interiors plus gregarious roosting of thousands of individuals in a single site reduces energetic expenditures while bats rest during the day. The cost bats pay for this type of roosting strategy is increased competition for food near the roost, which may be considerable, due to the large numbers of bats using the three major roosts in this study (peak numbers were over 20,000 at each roost, B. Alberti, pers. comm.). Bats flew commute distances up to 28.2 km to forage (Table 2), despite the presence of food resources much closer to roosts, perhaps to avoid competition for nectar at plants nearer the roost. Long-distance commuting may not be a serious disadvantage for bats of the genus *Leptonycteris*, however, because they have high wing loading and the greatest mass of all bats in the subfamily Glossophaginae (Sahley et al. 1993). Large body size reduces cost of transport (Brown et al. 1978) and high wing loading increases flight speed. These two morphological characteristics may be adaptations for fast, efficient flight during long distance travel (Norberg 1987).

Bat activity patterns differed appreciably during the two years of our study. Adults left day roosts over an hour earlier during 1999 when resources were low compared to 1998 when resources were high. This behavior likely reflects an increase in time needed to forage when few flowering *A. palmeri* are available (Part 3).

Sizes of home ranges and core use-areas were similar for bats in 1998 and 1999, despite large difference in density of flowering *A. palmeri* between years. This suggests that sizes of home ranges and core use-areas did not reflect differences in resource abundance between years. Furthermore, in 1999 home-range size did not vary with changes in density of flowering *A. palmeri* (Fig. 3). Thus, home-range size of lesser long-nosed bats is likely influenced by factors other than current levels of resource abundance at the landscape scale. For example, home-range size of adults decreased with increasing density of dead standing *A. palmeri* inflorescences (Fig. 3).

Density of flowering and dead standing *A. palmeri* in home ranges of adults was greater than that available on the landscape, and density of dead standing *A. palmeri* inflorescences in bat home ranges was similar each year. Therefore, bats seemed to select areas that had high food abundance as well as evidence of high food abundance in previous years.

Overlap in home ranges and even core-use areas among bats suggests that lesser long-nosed bats are

Table 7. Densities (plants/ha) of flowering *A. palmeri*, dead standing *A. palmeri*, and both combined within home ranges of lesser long-nosed bats, southeastern Arizona, 1998 and 1999.

Year	Age	Density of flowering <i>A. palmeri</i>			Density of dead standing <i>A. palmeri</i>			Density of flowering and dead <i>A. palmeri</i> combined		
		\bar{x}	SE	Range	\bar{x}	SE	Range	\bar{x}	SE	Range
1998	Adult	3.5	0.4	2.6-5.4	3.8	1.2	1.2-6.9	6.4	1.4	3.6-10.4
1999	Adult	0.8	0.4	0.2-3.0	3.4	0.3	1.4-6.6	4.3	0.5	1.6-9.3
1999	Juvenile	0.7	0.1	0.6-0.8	3.1	0.3	2.4-3.7	3.9	0.2	3.5-4.4

not territorial, unlike other nectarivorous bats, such as *Glossophaga soricina* (Lemke 1984). Individuals that were captured night roosting together fed at the same sites simultaneously, yet used different day roosts located far from one another. Although areas with densities of flowering *A. palmeri* as high as 9.9 plants/ha existed in the study site, bats returned repeatedly to the area near where they were initially captured while night roosting. This suggests that site fidelity and other factors besides density of flowering *A. palmeri* influence habitat suitability for lesser long-nosed bats.

Several aspects of juvenile bat behavior differed from that of adults. Juvenile core use-areas were larger than those of adults, which may reflect the lack of experience and inefficient foraging strategies of younger individuals. Young are born between early May and late June, and do not begin flying outside the maternity roost for another 6 weeks (Hoffmeister 1986). Although sample sizes were small, juveniles left roosts earlier and returned later than adults, suggesting once again that they were less efficient at acquiring food resources.

MANAGEMENT IMPLICATIONS

The location of suitable day roost sites and of flowering *A. palmeri* determines the distances bats must fly each night. *A. palmeri* is distributed patchily and the number of flowering plants varies greatly from year to year. We found evidence that bats select areas with both high resource abundance and evidence of high resource abundance in previous years, suggesting site fidelity to *A. palmeri* stands. The seasonal dietary specialization of lesser long-nosed bats on *A. palmeri* in southeastern Arizona implies that a reduction in or further fragmentation of *A. palmeri* populations could have serious effects on bat behavior, forcing them to commute farther, roost in substandard roosts, or compete with one another for food at remaining plants. These changes could eventually have adverse effects on the Arizona population of lesser long-nosed bats.

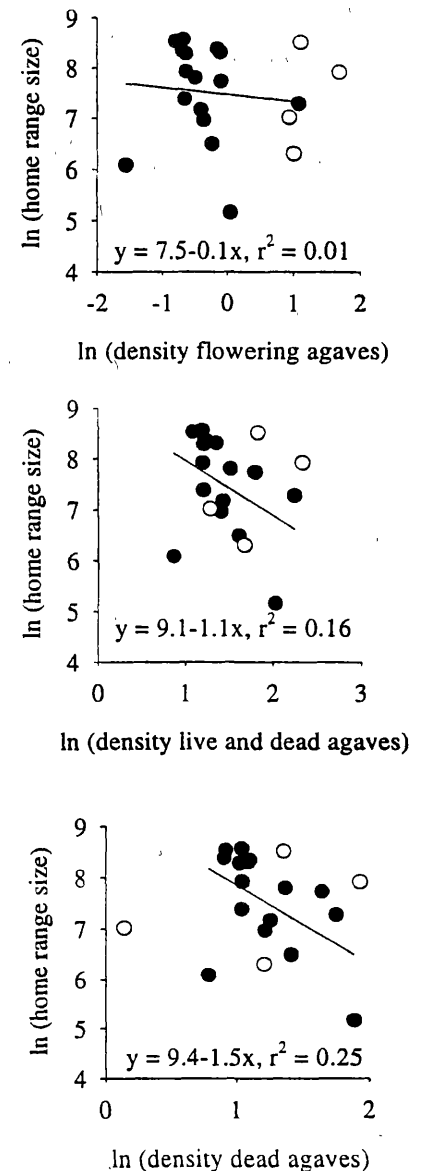


Figure 3. Regression of home-range size (ha) on density of flowering *A. palmeri*, density of dead standing *A. palmeri*, and density of both combined (plants/ha) for adult bats in 1999 (closed circles). Open circles represent data for adult bats in 1998.

Part 2: Foraging Behavior

To better understand how lesser long-nosed bats use food resources, we examined visitation rates of bats to *A. palmeri* near a roost of 10,000 lesser long-nosed bats. Our objective was to determine associations between characteristics of individual *A. palmeri* and rates of bat visitation.

METHODS

Observations took place in Coronado National Memorial, at the southern end of the Huachuca Mountains, along the border of the United States and Mexico. We selected a subset of flowering agaves for observations at distances of about 350 to 3,750 m from a known lesser long-nosed bat day roost site. Each night between 2 and 7 August 1999, we observed foraging behavior of bats simultaneously at 3 or 4 flowering *A. palmeri* using night-vision equipment, for a total of 170 observation hours. A tally counter was used to count number of contacts between feeding bats and open flowers.

We measured 8 structural and spatial characteristics of plants to assess their association with foraging patterns of bats: inflorescence height, total number of umbels, number of flowering umbels, relative vertical position of flowering umbels along the inflorescence, density of flowering *A. palmeri* within a 200-m radius of the focal plant, distance and direction from the bat roost, and elevation. Each inflorescence has 10-35 umbels that bloom sequentially from the bottom to the top of the plant. None of the focal agaves had flowering umbels in the upper portion of the inflorescence during our study. All focal plants were located either east or west of the bat roost because elevation soon exceeds that which is tolerable to *A. palmeri* north of the roost, and the study area borders Mexico to the south, an area to which we did not have access.

We analyzed variation in the number of visits per plant per hour using stepwise multiple regression, with a square root transformation applied to the number of visits per plant per hour to determine which characteristics were useful in explaining bat visitation rates. We also used principal components analysis (PCA) to ordinate related explanatory variables, and then regressed number of visits per plant per night (square root transformed) against the first 3 components to determine if these combinations of factors explained bat visitation rates further than individual factors.

RESULTS

Bat visitation rates ranged from 0 to 1023 visits per plant per hour, and averaged 273 visits per plant per hour (SE = 17, $n = 170$). The number of visits to each plant also varied throughout the night. The widest range of visits in one hour to one plant during one night was 21 to 1023.

Five of eight characteristics that we measured explained significant variability ($P < 0.05$) in bat visitation rates (Table 8). Time of night was most strongly associated with visitation rates which decreased as the number of hours after sunset increased (Fig. 4). Two spatial factors also were associated with visitation rates: visitation rates decreased as distance from the roost increased and was greater at plants east of the roost than at plants west of the roost (Fig. 4). Two structural characteristics of plants were associated with visitation rates: visitation rates increased as the number of flowering umbels per plant increased and increased as the relative position of the flowering umbels progressed from the bottom toward the middle of the inflorescence (Fig. 4). Inflorescence height, total number of umbels, density of nearby flowering conspecifics, and elevation did not explain any appreciable variation in bat

Table 8. Factors that explained variation in visitation rates ($P < 0.05$) of lesser long-nosed bats to *A. palmeri*, southeastern Arizona, 1999.

Factor	Estimate	p-value
Time of night (hr after sunset)	-0.79	<0.0001
Direction from roost (east or west)	-11.29	<0.0001
Distance from roost (km)	-0.002	0.0004
No. flowering umbels	1.20	0.0070
Relative vertical position of flowering umbels	7.31	0.0260

visitation rates ($P > 0.14$).

Three plant characteristics were correlated: total number of umbels and number of flowering umbels ($r = 0.67$), number of flowering umbels and plant height ($r = 0.72$), and plant height with total number of umbels ($r = 0.85$). When all 8 explanatory characteristics were ordinated to eliminate this intercorrelation, only the second principal component (21% of total variation) explained a significant amount of variation in number of bat visits per night ($P = 0.02$). This component reflected mostly differences in elevation and differences in direction from the roost (Fig. 5).

DISCUSSION

Visitation rates of lesser long-nosed bats to *A. palmeri* paralleled the trend in nectar production of the forage plant. Plants produce nectar between 2000 and 0600, with peak production at 2100 and a gradual decrease until dawn (Slauson 2000). Similar trends in nectar production are characteristic of other plants pollinated by lesser long-nosed bats, such as organ pipe cactus (*Stenocereus thurberi*) and cardon (*Pycnophloeus pringlei*) in northwestern Mexico (Fleming et al. 1996), as well as several species of columnar cacti in Venezuela (Nassar et al. 1997). In all of these plant species, the highest levels of nectar production coincides with the time of day when bats emerge from day roosts, when their energy demands are greatest.

The decrease in bat visitation rates as distance from the roost increased may be explained by two factors. First, the farther plants are located from the roost, the more energy bats must use traveling to them. Therefore, visiting plants closest to roosts minimizes energy expenditure. Second, as bats disperse from the roost in all directions, the area encountered increases exponentially with increasing distance, so the likelihood of bats detecting a flowering plant decreases. Therefore, plants closest to a roost should be visited more often than plants farther away.

Lesser long-nosed bats engage in two distinct foraging strategies. Some bats remain in close proximity (<4 km) to the day roost throughout the night, and some commute to foraging grounds as far as 28 km from their day roost where they spend the majority of the night foraging in a small area before commuting back to the day roost (Part 1). Individuals that use distant foraging grounds may need to visit plants relatively close to the roost to gain energy before beginning the commute, thus contributing to high visitation rates at plants close to the roost as well as to high visitation rates observed during the first few

hours after sunset.

Bat visitation rates differed between plants located east and west of the roost (Table 8, Fig. 5). The low number of bat visits to plants west of the roost compared to plants east of the roost may have reflected the low number of *A. palmeri* growing west of the roost. Oak woodland dominates areas to the west of the roost, whereas areas to the east are predominately grassland: *A. palmeri* grows much more densely in grassland than oak woodland (Gentry 1982). Lesser long-nosed bats select areas of relatively high agave density in which to forage (Part 1).

Visitation rates increased with the number of flowering umbels per plant. Plant species that rely on animals to transport pollen attract potential pollinators with visual or aromatic stimuli (Faegri and Van der Pijl 1966). An increase in size or abundance of these stimuli may attract more pollinators. Hummingbirds and insects visit large plants or large inflorescences more frequently than small plants or small inflorescences (Pyke 1981, Geber 1985, Cruzan et al. 1988).

Bat visitation rates also increased as the relative vertical position of flowering umbels progressed from the bottom to the middle of the inflorescence, and then decreased again as the vertical position of flowering umbels rose to the top of the inflorescence. This pattern may reflect bats responding to resource abundance at a small scale, as umbels in the middle of *A. palmeri* inflorescences tend to contain the most flowers (Slauson 1995) and thus likely provide the most nectar. Other studies have demonstrated that pollinators visit plants with many flowers more often than plants with few (Augspurger 1980, Real and Ratchke 1991). The pattern of visitation rates we observed may have been due to the attraction of pollinators to umbels with larger floral displays. Because we observed foraging activity over a short time period (6 nights), we eliminated the potential confounding effects of seasonal changes in behavior.

The two plant characteristics that were correlated with the number of flowering umbels, total number of umbels and plant height, were not useful in explaining the number of bat visits. Although correlated, exploring the relationship between these three variables and visitation rates helps distinguish

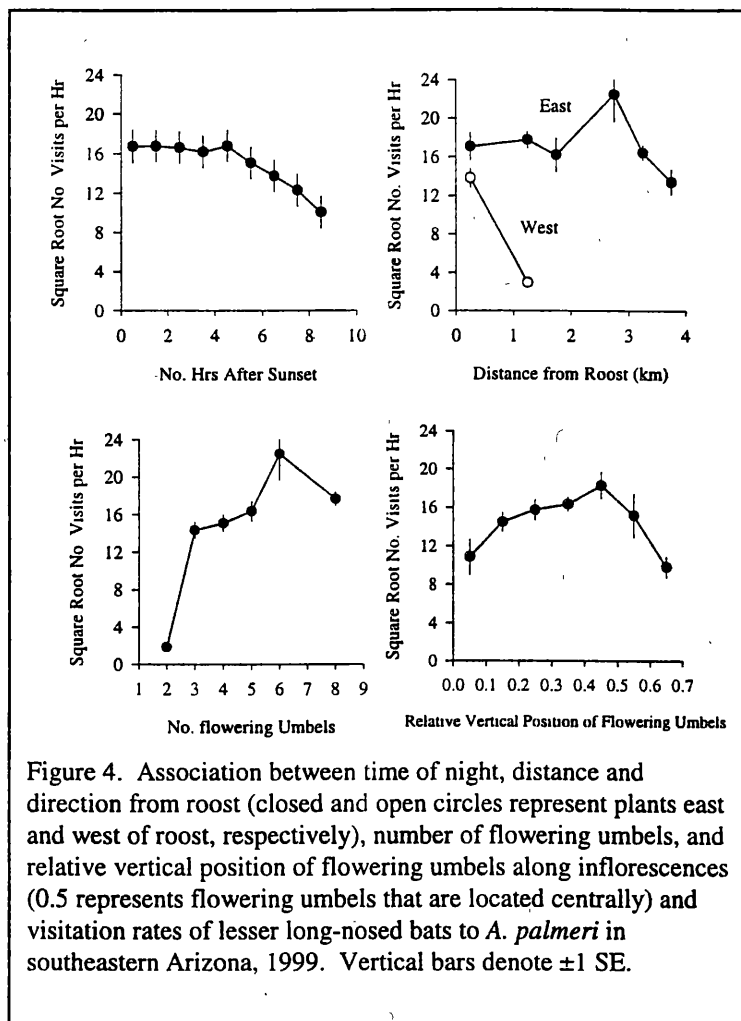
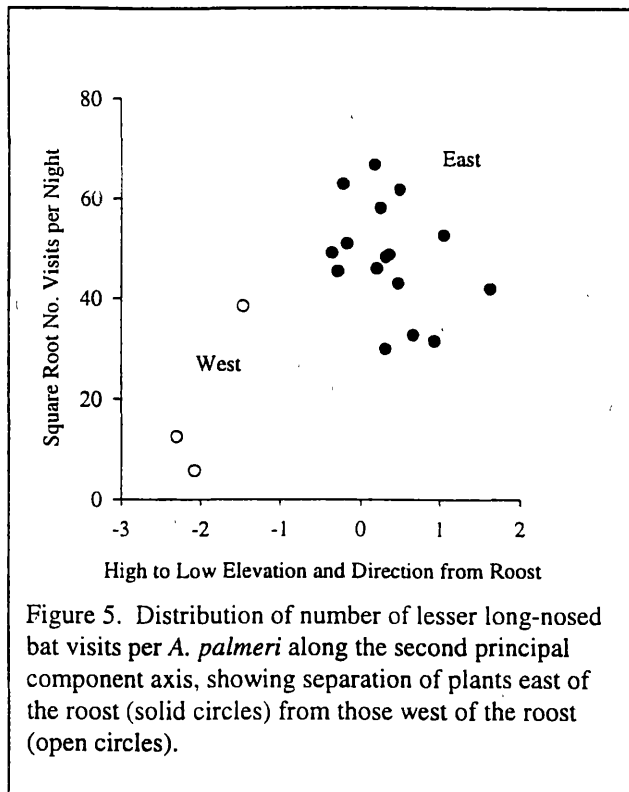


Figure 4. Association between time of night, distance and direction from roost (closed and open circles represent plants east and west of roost, respectively), number of flowering umbels, and relative vertical position of flowering umbels along inflorescences (0.5 represents flowering umbels that are located centrally) and visitation rates of lesser long-nosed bats to *A. palmeri* in southeastern Arizona, 1999. Vertical bars denote ± 1 SE.



which sense(s) bats use to select plants. If bats locate agaves with echolocation, they would likely detect taller plants more easily than shorter ones because the former rise above surrounding vegetation. Plant height did not explain visitation rates ($P = 0.20$). If bats locate agaves visually, they may detect plants with many umbels more easily than those with few umbels. Number of umbels did not explain visitation rates ($P = 0.65$). Finally, if bats locate agaves through olfaction, plants with more blooming flowers may be selected preferentially. Although we did not count the number of blooming flowers, the number of flowering umbels provides an estimate of this parameter. What is evident, is that the number of flowering umbels and the relative vertical position of those umbels (which is related to the number of flowers within those umbels) were two of the factors that best explained visitation rates (Table 8). These two factors provide cues as to the amount of nectar presently available to a pollinator.

A. palmeri is a big-bang producer that flowers only once during its 10-30 year lifetime, and dies shortly thereafter (Schaffer and Schaffer 1979). The number of plants within *A. palmeri* populations that flower each year oscillates considerably, as is the case with other desert perennials such as *Agave deserti* (Nobel 1992) and *Yucca elata* (Laslei and Ludwig 1985). Patterns of resource selection by bats will be best understood when studied under a range of resource-abundance levels. The number of flowering *A. palmeri* in our study area was low during our study ($\bar{x} = 0.8 \pm 0.4$ plants/ha, Part 1), so bats may have been less selective during the study than they would in years when more flowering plants were available. Visitation rates probably were relatively high at all agaves observed, partly because all focal plants were located within 4 km of a roost containing 10,000 bats. Therefore, we suggest further insight might be gained by examining visitation rates at plants located farther from major roosts and during years when a higher number of rosettes flower.

MANAGEMENT IMPLICATIONS

As humans populations increase, the amount of land in a natural state and thus the density of native plants decreases. The dietary specialization of lesser long-nosed bats on a single species of plant while in southeastern Arizona makes the bats vulnerable during their residence time, and thus it is important to determine what factors influence bat preferences for individual plants. We found that bat visitation rates to individual forage plants were influenced by both the location of plants relative to the bat roost, as well as the flowering stage of plants. Because flowering stage is a factor that changes over time and because of the sparse, patchy distribution of *A. palmeri* across the landscape, the conservation of lesser long-nosed bats is dependent upon the cooperation of a large number of land owners and resource managers.

Part 3: Energetics

Bats are small homeotherms with high metabolic rates. Because flight is the most energetically costly form of locomotion, bats must have low body mass, which prevents them from maintaining large energy reserves. Consequently, bats require a relatively energy-rich, constant food supply to meet their extraordinary energy demands.

To better understand the energetic requirements of lesser long-nosed bats, we examined their time-activity budgets. Our specific objectives were to determine daily energy expenditures (DEE) of bats and estimate the energy available from nectar of *A. palmeri*.

METHODS

Bat Behavior and Associated Energetic Costs

We estimated DEE for lesser long-nosed bats by measuring time-activity budgets in the field and using allometric equations or previously reported laboratory measurements of the energetic costs of these activities. We categorized bat behaviors into one of four activity types: day roosting, night roosting, commuting, or foraging. Time that bats spent engaged in each activity was estimated via radiotelemetry of 60 female lesser long-nosed bats (*Part 1*).

We estimated time spent day roosting by determining average time of emergence from and reentry to day roosts by radiotransmitted bats on 11 nights. We calculated average flight speeds by dividing the mean distance between day roosts and core use-areas (*Part 1*) by the mean time bats spent in flight between day roosts and core use-areas ($n = 21$ flights, 9 different bats), and then divided the mean of all known commute distances ($n = 23$) by mean flight speeds to arrive at an estimate of mean time spent commuting. We estimated time spent foraging and night roosting by tracking single bats continuously from emergence to reentry to day roosts ($n = 5$ nights, 2 different bats in 1998; $n = 4$ nights, 4 different bats in 1999). We determined time spent resting between foraging bouts by noting a constant radiotelemetry signal, which indicated no movement, and added this to time spent in caves and mines during the night to determine total time spent night roosting. We estimated time spent night roosting by averaging the proportion of time not day roosting or commuting that was spent resting. The remaining time was categorized as time spent foraging.

Floral Rewards

The volume of nectar produced and the concentration of sucrose in the nectar together determine the caloric reward flowers provide. We used nectar volumes measured at exclosed *A. palmeri* flowers in our study area (Slauson 1999). We averaged sucrose concentrations calculated from refractive indices of *A. palmeri* nectar obtained from exclosed flowers in our study area (Slauson 1995, 2000), converted to g sucrose per 100 ml solution (CRC Handbook of Chemistry and Physics 1978), and then multiplied by the energy value of sucrose (4.0 cal/mg sucrose; Heinrich 1975) to determine energy values provided by nectar (Bolten et al. 1979). We estimated total nectar production per plant over the course of a flowering season by multiplying mean nectar production per flower over the course of its lifetime by mean number of flowers per plant.

Sugar assimilation efficiency is near 100% in *Glossophaga soricina*, a bat closely related to lesser long-nosed bats (Winter 1998) and in hummingbirds (Lopez-Calleja et al. 1997) when feeding on sucrose solutions, so net energy intake of bats should closely approximate metabolizable energy.

RESULTS

Energetic Costs of Bat Activities

Basal rate of metabolism (BMR) of homeothermic animals is a measure of metabolism when animals are in a resting post-absorptive state at a temperature where no energy is expended for thermoregulation (Kunz 1980). Mean BMR for lesser long-nosed bats is 1.66 ml O₂/g/hr (Carpenter and Graham 1967) mean mass of the bats at our study site was 24.2 g (SE = 0.2, *n* = 107), and 1 liter O₂ = 4.8 kcal (McNab 1988), so mean energy expenditure of a resting bat at thermoneutrality is 0.193 kcal/hr. Observations of adult female lesser long-nosed bats in a maternity roost in southwestern Arizona showed that bats never slept while day roosting: individuals spent 75% of the day resting but alert and most of the remainder grooming (Fleming et al. 1998). Because metabolic rates of animals that are awake and not at thermoneutrality are commonly 1.25 times higher than BMR (King 1974, von Helversen and Reyer 1984), we multiplied BMR by 1.25 to arrive at a value of 0.24 kcal/hr for the energetic cost of day roosting.

Bats are alert and somewhat active while resting in night roosts and during short periods of non-flight activities between feeding bouts. Metabolic rates are probably higher during these time periods than while day roosting because bats are likely more vigilant in the more exposed night roost sites than in well protected day roosts, are not receiving the energetic benefits of communal roosting, and probably spend more time grooming because they recently collected pollen on their fur. Because metabolic rates of birds that are active but not in flight are approximately 1.7 times those of BMR (Wolf and Hainesworth 1971, King 1974), we multiplied BMR by 1.7 to arrive at a value of 0.33 kcal/hr to estimate the metabolic cost of night roosting.

We separated flight activities into commuting and foraging categories because commuting flights presumably consist of uninterrupted forward flight, whereas foraging flights involve changes in flight speeds and directions as well as momentary hovering and are consequently more energetically costly. To calculate energy used during commuting flights we used Thomas's (1975) formula: $\text{Power}_{\text{horizontal flight}} = 50.2 \text{ Mass}^{0.79}$ which yields 2.65 kcal/hr.

To determine energy expenditure during foraging flights, we used Winter and von Helversen's (1998) formula for metabolic flight power, which was based on laboratory measurements of 6 nectarivorous bat species, including lesser long-nosed bats, while foraging in wind tunnels: $\text{Power}_{\text{foraging flight}} = 50.2 \text{ Mass}^{0.771}$. We thus estimated energy expenditure for foraging flight to be 2.85 kcal/hr.

Daily Energy Expenditure

Although bats spent approximately the same amount of time ($\bar{x} \pm \text{SE}$ hrs) day roosting (16.7 ± 0.2) and commuting (1.1 ± 0.1) in 1998 and 1999, time spent foraging and resting varied greatly between years (Table 10). During 1998, bats spent an average of 6.1 hrs (SE = 0.4) away from day roosts but not commuting; 38% (2.3 hrs) of this time was spent foraging and 62% (3.8 hrs) was spent resting. During 1999, bats spent an average of 6.4 hrs (SE = 0.2) away from day roosts but not commuting; 80% (5.1 hrs)

of this time was spent foraging and 20% (1.3 hrs) was spent resting. Therefore, estimated DEE was 14.59 kcal/bat/day during 1998 and 21.91 kcal/bat/day during 1999.

Floral Rewards

Mean nectar production estimated from 290 *A. palmeri* plants in 1998 was 2.56 ml/flower over the course of each flower's lifetime (Slauson 1999). Mean sucrose concentration from 40 *A. palmeri* flowers was 15.7% (Slauson 1995, 2000), which represents 0.67 kcal/ml nectar. During its lifetime, each flower therefore provided 1.72 kcal. In the region we studied, mean number of flowers per plant was 1905 (Slauson 1995), so each plant provided an average of 3277 kcal over the course of its flowering lifetime.

Lesser long-nosed bats typically reside in the study area for a maximum of 2 months, between late-July and late-September, although numbers of bats fluctuate and most individuals reside <2 months. If we assume maximum DEE for each bat is approximately 22 kcal, and that each bat will be in the area for a maximum of 60 days, each bat requires a maximum of 1320 kcal during its stay. Because bats are present only during 2 months of the plants' 3 month flowering period, an average *A. palmeri* plant could provide bats with 2185 kcal ($3277 \text{ kcal} \cdot \frac{2}{3}$). Therefore, assuming no nectar loss to other sources, each plant could supply almost all the energy required to support more than 1.5 lesser long-nosed bats (2185 kcal/1320 kcal) during their 2-month stay in southeastern Arizona.

Our best estimate of the maximum number of bats at 3 major roosts within our study area at peak population levels is approximately 100,000 individuals. Commute distances for bats ranged from 2.8-28.2 km and averaged 18.9 km (Part 1), so a circle with radius 20 km probably encompasses most bat foraging activities. This circle has an area of 1257 km², so the total area likely to be visited by bats from all 3 roosts is 3771 km². If 100,000 bats need 60,412 flowering *A. palmeri* to survive the summer, mean density of flowering *A. palmeri* across the entire 3771 km² area near the roosts must average ≥ 0.16 plants/ha.

DISCUSSION

Our Results

Energy expended by lesser long-nosed bats varied with annual differences in availability of food resources. Bats spent 120% more time foraging and 66% less time night roosting in 1999 than in 1998. This large annual difference in activity is likely explained by the large difference in density of flowering *A. palmeri* between years (Part 1). The time and energetic cost of feeding on nectar depends on the abundance and distribution of flowering plants. In 1999, bats presumably had to spend more time foraging because flowering plants were less abundant than in 1998, and more bats may have been feeding at each plant, potentially reducing resources, on average, at each plant. Our results suggest that small differences in activity budgets can alter energy requirements drastically.

Previous Studies

Previous estimates of energy requirements for lesser long-nosed bats vary widely. Petit and Pors (1996) used allometric equations derived to predict energy requirements of eutherian mammals and passerine birds (from Nagy 1987), attempting to bracket the true energy requirements for bats. Their

estimate of DEE for non-pregnant female lesser long-nosed bats was between 11.29 and 24.30 kcal/day, which includes our estimates (Table 9).

Howell (1979) and Horner et al. (1998) calculated daily energy budgets for lesser long-nosed bats and arrived at estimates similar to one another but different from that of Petit and Pors (1996) and ours (Table 9). Although Howell used methods similar to ours to estimate cost of night roosting and cost of flying, she arrived at a lower estimate for overall flight costs than we did because she did not acknowledge that foraging flight requires more energy than commuting flight. Howell also did not adjust BMR, as we did, to estimate the cost of day roosting, which is necessary because bats are not completely inactive, in post-absorptive state, or in thermoneutrality while day roosting. Furthermore, Howell used mean body mass of unfed bats (17 g) whereas we used the more realistic mean body mass of bats captured throughout the night with varying amounts of food in their stomachs (24.2 g), so the allometric equations used to calculate energetic costs for night roosting, day roosting, and foraging produced appreciably lower estimates in her study than in ours.

Horner et al. (1998) used different scaling parameters than we did to estimate costs of day- and night-roosting from BMR, with no justification for their choices; scaling parameters from other bat and bird energetic studies were higher. Furthermore, Horner used estimates of mechanical power output derived from aerodynamic theory to calculate costs of commute and forage flights, which are known to underestimate the physiological requirements of flight (Tatner and Bryant 1986). Flight costs predicted through allometric equations such as Tucker (1973) ($\text{Power} = 55.7 \text{ Mass}^{0.78} = 3.06 \text{ kcal/hr}$) and Berger and Hart (1974) ($\text{Power} = 0.29 \text{ Mass}^{0.72} = 2.88 \text{ kcal/hr}$) estimate flight costs more similar to the costs we used ($\text{Power}_{\text{commute}} = 2.65 \text{ kcal/hr}$, $\text{Power}_{\text{forage}} = 2.85 \text{ kcal/hr}$) than to those used by Horner ($\text{Power}_{\text{commute}} = 0.90 \text{ kcal/hr}$, $\text{Power}_{\text{forage}} = 0.83 \text{ kcal/hr}$).

Because it was difficult to determine with certainty the amount of time bats spent foraging relative to time spent resting between foraging bouts via telemetry, we also used allometric equations to predict DEE as a way to double-check the reasonability of our estimates (Table 10). The low value predicted for bats by Kunz (1980) has underestimated actual energy requirements of other bats by a factor of 2 (von Helversen and Reyer 1984), so it is not surprising that our estimates exceeded the value predicted by this formula. Our estimate of DEE is higher than that obtained by Nagy's (1987) equation for eutherian mammals, and lower than those predicted by equations from Walsburg (1983) and Nagy (1987) for passerine birds. DEE for nectarivorous bats determined in the field and in the laboratory are usually 60-70% higher than the allometric average reported for terrestrial mammals (Winter 1998), yet less than those of birds (Winter and von Helversen 1998). Therefore, we believe our estimates are reasonable.

MANAGEMENT IMPLICATIONS

The high energy demands of bats coupled with the small amount of nectar available per flower forces bats to visit many flowers each night. The high amount of annual variability in the number of flowering *A. palmeri* may make food gathering easy during years when many plants bloom, allowing bats more time to rest, while forcing bats to spend more time foraging and allowing less time to rest during years when few plants bloom. DEE of lesser long-nosed bats may be almost 1.5-2 times as high as values previously reported, and thus the amount of food needed to support the bat population in southeastern Arizona may be much greater than thought previously. Consequently, maintaining sufficient numbers of

Table 9. Comparison of daily energy expenditure (DEE) calculations for lesser long-nosed bats from this and previous studies.

Day roosting		Night roosting		Commuting		Foraging		DEE (kcal)	Reference
Time (hr)	Cost (kcal/hr)	Time (hr)	Cost (kcal/hr)	Time (hr)	Cost (kcal/hr)	Time (hr)	Cost (kcal/hr)		
16.85	0.24	3.82	0.33	1.01	2.65	2.32	2.85	14.59	present study-1998
16.47	0.24	1.30	0.33	1.13	2.65	5.10	2.85	21.91	present study-1999
14.00	0.14	7.00	0.24	-	-	3.00	2.01	9.67	Howell 1979
18.00	0.275	1.00	0.343	1.83	0.902	3.17	0.833	9.58	Horner et al. 1998

Table 10. Calculations of daily energy expenditure (DEE) of lesser long-nosed bats using allometric equations.

Formula	Organisms to which formula applies	Estimated DEE (kcal/day) for 24.2 g bats	Reference
$DEE = 184.5 \times \text{Mass}^{0.7674}$	bats	10.61	Kunz (1980), equation 4
$DEE = 203.6 \times \text{Mass}^{0.6052}$	birds	21.42	Walsburg (1984), equation 8
$FMR = 3.35 \text{ Mass}^{0.813}$	eutherian mammals	10.66	Nagy (1987), table 3
$FMR = 8.88 \text{ Mass}^{0.749}$	passerine birds	23.05	Nagy (1987), table 3

Agaves as a food source for bats and other nectivores is likely considerably more important than thought previously.

Part 4: Recommendations for Future Research

For our results to aid recovery of lesser long-nosed bats in the Southwestern U.S., the scope of inference we investigated must be expanded both spatially and temporally. The spatial scope of our results is limited because the population of bats we radio-marked were captured in a small geographic area and while night roosting together. Subsequently, most individuals foraged near the capture location and near one another. Further, Agave resources vary in abundance considerably among years, as exemplified by the high variation we observed in our study of only two years. Subsequently, increased observations over several years—which would likely cover a range of resource abundances—would also increase inferences. Therefore, patterns of resource selection by bats will be best understood when studied over a longer time period and larger geographic area.

Therefore, we recommend further study of lesser long-nosed bat movement patterns at other roosts to determine if the resource-use trends we observed are consistent in time and space. We recommend that future studies radio bats from day roosts to determine if bats that day roost together show a wider range of commute distances than those that night roost together, such as those we observed. We also recommend further investigation into the issue of fidelity of individual bats to specific foraging areas, and the potential effects that changes in land-use practices may have on these behaviors. With the rapid rate of development in southern Arizona, this issue may be paramount to continued persistence of nectar feeding bats in this region.

Further insight into bat preferences for individual plants would be gained by examining visitation rates to forage plants during years when a higher number of rosettes flower, when bats can be more selective of which plants they visit. Observing plants located farther from major roosts would help establish if bats show the same degree of preferences when they commute farther distances and require more energy than the bats we observed, which was at location relatively close to the roost site.

A more accurate assessment of the amount of energy available to bats from Agaves could be obtained if the amount of *A. palmeri* nectar extracted by animals other than lesser long-nosed bat was determined, so we suggest this as a future goal of Agave studies. Lastly, techniques based on doubly-labeled water would help to determine energy intake and expenditure independently for these nectar feeding bats, information that would further refine establishing their resource needs in this region.

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